MANTER: Journal of Parasite Biodiversity (ISSN 2470-8224)
Occasional Papers, Number 30, December 30, 2022
doi: 10.32873/unl.dc.manter30
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This article has been produced in support of and with appreciation for the efforts by Gábor Földvári of the Institute of Evolution, Centre for Ecological Research, and the Centre for Eco-Epidemiology, National Laboratory for Health Security (both located at 1121 Budapest, Konkoly-Thege Miklós út 29-33, Hungary). Through his untiring efforts, team building, and leadership, he has secured the first EU-wide team research grant. This work was supported by the National Research, Development and Innovation Office in Hungary (RRF-2.3.1-21-2022-00006) and the COST Action CA21170 "Prevention, anticipation and mitigation of tick-borne disease risk applying the DAMA protocol (PRAGMATICK)," which represent the first funded efforts to apply the principles of the DAMA protocol.

Perspective

Let Emerging Plant Diseases Be Predictable

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Abstract

A prevalent concept for colonization and evolution among plant pathogens and their hosts stems from a post-Darwinian paradigm rooted in the formalized assumption of "specialized parasitism." Seminal studies on rust fungi of socioeconomic importance integrated such an evolutionary perspective driven by the assumption of strict coevolution among pathogens and their plant hosts. Following this fundamentally unfalsifiable assumption, theories regarding host-switching for parasites were dismissed. If colonization occurred, this process would depend upon the origin of specific and novel mutations that allow infections of previously unexploited hosts or host groups, the acquisition of a broader host range. After a specific mutation arose, parasites and hosts would be locked into an eventual evolutionary dead end (e.g., codified under Dietel's Law). Accordingly, if the parasites are highly specialized (one parasite, one plant), then new associations are rare or otherwise unpredictable. Similar schools of thought became dominant for animal pathogens and were established during the same period (i.e., Müller's rule, Fuhrmann's rule, and Fahrenholz's rule). Other studies that focused on plant pathogens took the one host–one parasite idea for granted and only tentatively included evolutionary insights in subsequent development of plant pathogen scientific frameworks. Later, emerging from neo-Darwinian views, the paradigm of strict cospeciation was conflated with the gene-for-gene rule postulated in 1956 and which has persisted among phytopathologists even to the present day. In a parallel history, conceptual development among plant pathologists and parasitologists has assumed that colonization is rare and cannot be predicted, given the dependence on the origin of the elusive special mutation. In contrast, current impacts and increasing frequency of emerging pathogens and epidemics across the globe, which influence health and food security, suggest that this historical approach fails in describing a complex biosphere in dynamic change. The Stockholm paradigm (SP) provides a

powerful alternative to what may be regarded as the standard model of coevolutionary diversification. The SP creates a theoretical workbench from which emergence of new associations can be evaluated and predicted. The SP provides a new perspective in exploring the dynamics among the phytoplasmas, an emergent group of plant pathogens with substantial risk for food security. New insights are examined, pushing for resolution of the internal conflicts generated by assumptions of the standard coevolutionary model, which has dominated the scientific reasoning for more than a century of plant pathology research.

Keywords: plant pathogen, crops, Stockholm paradigm, DAMA protocol, specialized pathogen, generalized pathogen

Introduction

The general failure of the current methods used to cope with emerging infectious plant diseases (EIPDs) stems from the prevailing idea that because of continued host-parasite specialization, each species of pathogen is considered to be tightly associated with its host (see Brooks et al., 2019 for a review). Although this paradigm of increasing specialization of parasites with their hosts is well known in the case of zoonoses, it is also the dominant paradigm in the discipline of plant pathology, with its origin in the earliest studies on rust fungi (Uredinales) and followed by the same trend of popularity during the last century.

The idea of specialized parasitism was first formalized by J. Eriksson (1894), who proposed to distinguish morphologically identical species by the allocation of biotypes named *formae speciales*. Other authors proposed similar concepts (reviewed by Ward, 1905) and all were following the notion suggested by de Bary (1863), when he first came up with the idea that rust fungi have to be classified according to their tendency to establish intimate unique relationships with one host, that is, *le choix rigoureux*. In the meantime, Plowright (1896) defined two points of view for the study of pathogenic fungi: (1) the herbarium viewpoint and (2) the laboratory viewpoint, thus setting the stage and establishing an artificial dichotomy between basic and applied research in plant pathology. He also stated that: "On the other hand those interested in plant diseases who look at the matter from a laboratory-view-point when they find one fungus on wheat and another on *Triticum repens* which, although they are indistinguishable by the eye, yet cannot be made to interchange hosts: they naturally regard them a distinct species" (Plowright, 1896).

This convenient and expedient distinction soon became a rule, which was supported by several researchers, also from an evolutionary standpoint. The belief that hosts and rust parasites reflect each other's ages of origin was first supported anecdotally by Dietel (1904), who provided arguments to support that the Uredineae ". . . have evolved *pari passu* with the plants upon which they are parasitic and, as a corollary, that when a mutation took place, leading to a change of host, it was almost always in the direction of selecting the new one from a group of later (or at any rate, not of earlier) evolution than the original host" (Grove, 1913). This assumption was embraced as Dietel's Law by many researchers for the entire last century (e.g., Savile 1968, 1971). Although several, not fully understood, exceptions to the rule were observed, they were eventually interpreted as apparent associations, and events of host-switching by a pathogen species were explained by the nature of the host rather than the nature of the pathogen (see the example of *Puccinia carici* and *P. urtica* in Grove [1913]).

This concept was in partial contrast with another idea formalized earlier by Darwin in his *The Origin of Species* (1872), that is ". . . the nature of the organism and the nature of the conditions. The former seems be much more the important . . ." Since then, the validity of the prevailing law about plant-pathogen coevolution was corroborated by means of experimental trials. For example, using an unknown biological form of rust, Stakman (1924) stated: "As wheat, oats, and rye apparently are immune, and barley nearly so, the rust could not be the *tritici*, the *avenae* or the *secalis* variety. It therefore must be *P. graminis poae*." Unfortunately, in these experiments, spatial and temporal variation were not taken into consideration.

Another idea that flourished toward the end of the 19th century and took hold solidly through the 20th century postulated that the trend of the evolutionary changes of the pathogens must lag behind that of their hosts and must evolve from the more complex to the simpler form, which in the case of rust means the move from heteroecious to autoecious forms (Savile, 1971). For decades, the phylogeny of this group of plant pathogens, as well as for

other group of pathogens such as bacteria, has been inferred based on the range of host species and spore or colony morphology; however, beginning in the middle of the 20th century, the genomic revolution helped to reconstruct evolutionary relationships and genealogies of several groups of microorganisms (Gupta, 2016), including members of the uncultured microbiome (Liu et al., 2022). Nevertheless, the influence of the post-Darwinian paradigm further supported by the gene-for-gene rule postulate in 1956 (Flor, 1956) persists among phytopathologists even to the present day.

Despite the lack of an extensive fossil record for several groups of plant pathogens, such as bacteria and fungi, the earlier phylogenetic reconstructions were calibrated by considering the fossils of the host plants (e.g., Savile, 1976). The evolutionary diversification of plant pathogens, in particular groups of non-free-living or nonsaprophytic organisms, was thought for a long time to be firmly tied to their hosts, further supporting Dietel's Law (Clay, 1988). Similar rules were established for animal pathogens/parasites (i.e., Müller's rule [Müller, 1871], Fuhrmann's rule [Fuhrmann, 1908], and Fahrenholz's rule [Fahrenholz, 1913]), and all were defining that group of parasites as often being associated with hosts that are closely related and that the pathogen's phylogeny mirrors the host's phylogeny. At the end of the 1930s, Ass (1939) suggested that the various rules and laws had no absolute value, and, among others, he provided an example referring to the plant parasite Uredinales (rust fungi). He defined first and second kinds of specificity depending on the degree to which the parasite or pathogen was locked to or associated with its host (Ass, 1939). Researchers in this area accepted previous laws and rules of specificity with scientific blinders that made them unable to see other alternative explanations for the patterns that were being discovered. This resulted in development of the paradoxical idea of pathogen/parasite–host specialization, which is a dead-end evolutionary pathway that taken to its ultimate conclusion would result in the pathogen/parasite being unable to acquire new hosts.

Despite this earlier tentative move to suggest alternative hypotheses, we had to wait several years before a new paradigm was formulated for animal pathogens (reviewed in Brooks et al., 2019), under which both animal and plant pathogens/parasites are able to survive in sloppy fitness space, defined as a loose-fitting ecological niche that includes many potential spaces (potential hosts) that could be occupied by a pathogen or parasite but are not yet colonized (Agosta and Klemens, 2008). In their exploring stage, pathogens may colonize new hosts by host-switching through resource tracking (the pathogen colonizes a different host by tracking phylogenetically conserved traits) or ecological fitting (the pathogen adapts to the new resource or host traits even if it is not the optimal fitness space) (Agosta, 2006; Agosta and Klemens, 2008). These concepts had not been applied to plant pathogens until recently, although a very similar concept was postulated by Morris and collaborators (Morris et al., 2009) for sapronose diseases caused by pathogenic microorganisms that inhabit aquatic ecosystems and/or soil rather than a living host. Morris et al. (2009) suggested a change in the paradigm about the evolution of plant pathogens by introducing the concept of "dual-use traits and exaptation." In animal pathology, such a fundamental change in paradigm and terms to describe how pathogens and their hosts evolve were suggested earlier (Brooks, 1979) and further generalized for all the types of associations in a comprehensive new paradigm named the Stockholm paradigm (SP) (Brooks et al., 2019). The SP is supported by an increasing amount of real-world data (e.g., among the more recent, Boeger et al., 2022) and theoretical models (reviewed in Souza et al., 2022).

In the following section, I discuss our ongoing research program at the University of Illinois at Urbana-Champaign designed to test the SP. By using phytoplasmas, a group of vector-borne pathogens, and their hosts as a study model, we aim to use the DAMA protocol, a policy extension of SP designed to Document, Assess, Monitor, and Act, as a workbench to predict emerging phytoplasma diseases.

The new paradigm for emerging phytoplasmas (bacteria) diseases

Phytoplasmas are a diverse group of obligate intracellular bacterial parasites (phylum Mycoplasmatota, class Mollicutes) that inhabit the phloem of vascular plants and are spread from plant to plant via sap-feeding hemipteran insects (Weintraub et al., 2019). Phytoplasma diseases affect more than 1,000 plant species worldwide, including major staple and cash crops and ornamentals, causing billions of dollars in annual losses (Brooks et al., 2021).

Most prior knowledge of this group of bacteria has been accumulated through studies aimed at controlling the spread of phytoplasma diseases of economically important plants. Because these bacteria are as yet not amenable to growth in culture media, a polyphasic approach for accurate identification and taxonomic designation is hampered, and phytoplasma classification is based mainly on genotypic data collected using a combination of molecular biology techniques. The classification scheme based on the *16S rRNA* gene enabled the description of more than

150 distinct subgroups (with an alphabetic designation) allocated in 37 groups (designated with a roman numeral) during the last 30 years. Almost all of them were discovered on domesticated plants (crops and ornamentals) that showed symptoms indicating phytoplasma presence.

Associations with plants

Known phytoplasmas are distributed worldwide and are known to infect nearly 1,000 plant species in about 100 families (Trivellone, 2018), with many apparently restricted to particular biogeographic regions and/or plant families (Trivellone, 2019). Network analysis of the co-occurrence of 16S rRNA phytoplasma groups with their plant hosts indicates that the associations are significantly modular and nested (Trivellone and Flores, 2019). Thus, phytoplasma-host associations tend to be specialized, with each group infecting a specific array of plants. Only three groups (16SrI, II, and XII) are associated with relatively large numbers of families and plant species (75, 36, 44 families and 201, 106, 116 species, respectively). However, these results are almost certainly biased by a lack of data on phytoplasma prevalence in asymptomatic plants in natural areas (Zwolińska et al., 2019; Trivellone et al., 2021; Trivellone, Cao, et al., 2022).

Associations with insects

Although phytoplasmas have been detected in many phloem-feeding hemipteran species that have fed on infected plants, insects capable of acquiring phytoplasmas may be incapable of transmitting them from plant to plant; that is, they are dead-end hosts for the phytoplasmas (Galetto et al., 2019; Trivellone et al., 2019). For plant-to-plant transmission to occur, phytoplasmas must be acquired by the vector, cross the midgut membrane, enter the hemolymph, replicate, migrate to the salivary gland, and enter the saliva prior to feeding by the vector on a different plant (Hogenhout et al., 2008; Huang et al., 2020; Koinuma et al., 2020). An insect that successfully transmits a pathogen from plant to plant is considered a competent vector. About 200 insect species across 13 families of Hemiptera, including Auchenorrhyncha, Fulgoromorpha, Cicadomorpha, and Psylloidea (see Trivellone, 2018) are reported to be associated with phytoplasmas, but fewer than half of them have been shown to be competent vectors. Known phytoplasma vectors are scattered among several distantly related lineages. Most known insect vectors are leafhoppers (Cicadellidae); fewer planthoppers (Fulgoroidea) and only two genera of jumping plant lice (Sternorrhyncha: Psyllidae) are known to act as phytoplasma vectors (Weintraub et al., 2019). Phytoplasma-vector associations have an apparently tight host-parasite linkage, with particular vectors associated with particular phytoplasmas. Leafhoppers that are known vectors span non-sister group taxa across a few subfamilies, tribes, and genera (Trivellone et al., 2017; Trivellone, 2019), suggesting that vector competence is rare and the ability to successfully transmit phytoplasmas has evolved independently multiple times (Dietrich, 2013). Several hemipteran genera include multiple vector species (Dietrich, 2013), suggesting that vector competence can be an evolutionarily conservative trait maintained through multiple speciation events. Many of the better-studied strains appear to be associated with a single competent vector species or genus. Only a few phytoplasmas (e.g., 16SrI and XII) have multiple reported potential and competent vectors (in 5 and 9 families and 77 and 65 species, respectively) (Trivellone, 2018, 2019). Particular groups of phytoplasmas also exclusively interact with particular groups of vectors (e.g., phytoplasmas in 16SrX group and Psylloidea spp.). Unfortunately, because most screening for phytoplasmas has focused on plants, and transmission trials are difficult and time consuming, vectors remain unknown for more than 85% of known phytoplasma strains.

A previous network analysis of phytoplasma-host associations for each biogeographic region revealed that 50 years of data collected in anthropogenic areas are defined by a specific structural pattern (Trivellone and Flores, 2019). Specifically, the proportion of realized associations to all those with potential is very low, indicating that the association in the anthropogenic areas tend to be highly specialized (one crop, one pathogen). Moreover, the realized associations are significantly modular and nested, with most of the modules involving a single phytoplasma group. Overall, the analyses carried out in agro/urban ecosystems are defined by a local or regional isolation for many associations, suggesting a recent co-evolutionary history. Indeed, on closer examination of the distribution of the number of subgroups in each group, half of the described groups include one subgroup only, most of them described in the last 15 years or never detected again after their first description. It has been hypothesized that this may be because these phytoplasmas are rare or the sequences representing these groups contain errors (Wei and Zhao, 2022). Although this could be a possible explanation, another more plausible cause could be that a large portion of the biodiversity of phytoplasmas in natural areas has been overlooked during the last half-century of research (Trivellone and Dietrich, 2021; Trivellone, Cao, et al., 2022). The pervasive, prevailing post-Darwinian assumption on the evolution of plant pathogens was inherited

without reflection and has driven most of the studies on phytoplasmas and phytoplasma-associated diseases, with some exceptions (such as Cvrković et al., 2022).

Our preliminary studies strongly suggest that natural areas worldwide harbor a diverse and largely undocumented phytoplasma biota (Trivellone et al., 2021; Wei et al., 2021; Trivellone, Cao, et al., 2022). By screening the 0.4% of potential insect phytoplasma hosts collected in natural areas and preserved in our biorepository at the University of Illinois (USA), we described 11 new strains, 42 new potential insect vector species, and 20 new country records for previously known strains. Ultimately, the purpose of our investigation is to evaluate the phylogenetic relatedness of phytoplasma hosts, the ecological fitness space for phytoplasmas (realized and potential)—which includes microhabitat preferences and transmission dynamic information—biogeographic insights, and the influence of environmental changes in shaping the phytoplasma-host associations. Data related to these associations are combined into the SP, which has been used here as a cognitive workbench that allows us to predict new potential associations and patterns of expansion or contraction in the suite of hosts of phytoplasmas. As shown earlier and reviewed in Hoberg, Boeger, et al. (2022), the DAMA protocol will generate scientific, actionable knowledge in order to predict emerging phytoplasma diseases.

The classic example of the emergence of the phytoplasma disease caused by *Flavescence dorée* that devastated the viticulture and wine industry during the end of the 20th century has been discussed in detail by several authors, and the SP describes how the emergence could have been anticipated (Brooks et al., 2021; Trivellone and Dietrich, 2021). But evidently the times were not ripe for a great change in the way to cope with emerging phytoplasma diseases. Recent genomics breakthroughs and advances in bioinformatics have spawned a huge amount of information; what we need to do now is use it with the evolutionary perspective suggested by the Stockholm paradigm.

Conclusion

Pathogens that cause diseases in crops are mostly well studied from the perspectives of plant disease epidemiology and management, but new diseases continue to emerge worldwide (Brooks et al., 2021). The wild origin of many pathogens has only recently been documented, and the existence of diverse assemblages of potentially pathogenic organisms in nature is only beginning to be revealed (McCann, 2020; Morens and Fauci, 2020; Boeger et al., 2022). Disease outbreaks often result from potentially pathogenic microbes that are widespread in nature becoming exposed to new hosts as a result of anthropogenic disturbance (Brooks et al., 2019, 2021; Trivellone, Hoberg, et al., 2022). As accentuated by increasing ecological fitting of pathogenic organisms into humans, plants, and domestic and wild animals due to human incursions into natural habitats, knowledge of the distributions and native hosts of potentially pathogenic microbes remains extremely rudimentary, and thus efforts to control disease outbreaks remain largely reactive (Brooks et al., 2021; Molnár, Hoberg, et al., 2022; Molnár, Knickel, et al., 2022; Trivellone, Hoberg, et al., 2022). Improved knowledge of the diversity, distribution, ecology, and phylogeny of microbial lineages known to be pathogens will be crucial to the development of proactive strategies for predicting and avoiding future outbreaks. Documenting pathogens in wildlands and human-modified habitats and their interfaces, and identification of global hotspots of pathogen diversity will contribute to achieving risk assessment of emergent infectious disease within the context of international trade and global environmental change (Hoberg, Boeger, et al., 2022; Hoberg, Trivellone, et al., 2022). Lack of knowledge on how pathogen diversity evolved and is maintained hampers our ability to manage severe diseases, the transmission of which is shaped by ecological interactions between multiple strains through networks of multiple vectors and host populations, as for example for vector-borne pathogens such as phytoplasmas (Pedersen and Fenton, 2007; Cator et al., 2020).

All pathogens and parasites obey the same suite of natural rules; however, each scientific discipline biased the interpretation of phenomena by assigning an elective host to each pathogen; the host that matters the most and/or the one that generates a profit are the economically important ones. This leads us to ignore a large portion of habitats colonized, the actual life histories, and the eco-evolutionary implications. To overcome this impasse, I argue that anticipating emerging plant diseases requires: (i) taking the pathogen's point of view with its entire pathway of spreading across the biosphere; (ii) a unified paradigm to improve interconnection among disciplines, theories, and hypotheses; and (iii) a clear operational workbench based on recursive procedures to aid the policymakers in adjusting the guidelines and mobilizing stakeholders to take action.

Acknowledgments – The author thanks Christopher H. Dietrich and an anonymous reviewer for their insightful suggestions and careful reading of the manuscript.

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